

A review: chemical ecology of *Ips typographus* (Coleoptera, Scolytidae)

SUN Xiao-ling^{1,2}, YANG Qing-yin³, Jonathan David Sweeney⁴, GAO Chang-qi⁵

¹ School of Forestry, Northeast Forestry University, Harbin 150040, P.R. China

² School of Life Sciences, Jilin Normal University, Siping 136000, P.R. China

³ General Forestry Protection Office of Liaoning Province, Shenyang 11002, P.R. China

⁴ Natural Resources Canada, Canadian Forest Service P.O. Box 4000 Fredericton, N.B. E3B 5P7, Canada

⁵ Jilin Provincial Academy of Forestry Sciences, Changchun 130031, P.R. China

Abstract: Chemical ecology of the spruce bark beetle *Ips typographus* (L.) was reviewed. The outbreak of *I. typographus* in central Europe triggered extensive research on chemical ecology. Males initiate host location and produce semiochemicals which attract both males and females. A successful mass attack must first overcome the resistance of the host tree. Pioneer *I. typographus* evolved to use the resin flow of host trees as kairomones in host location, and synthesized semiochemicals initially to detoxify the resin. If small bark beetle populations infest healthy trees, mass attack is prevented by host resistance. Nine monoterpene alcohols were found in male hind-guts, including *cis*-verbenol (cV) and 2-methyl-3-buten-2-ol (MB) which are regarded as primary aggregation pheromones, and a low proportion of Ipsdienol (Id) which increases attractiveness of cV and MB. Verbenone (Vn) and Ipsenol (Ie) are anti-aggregation pheromones, that play important roles in adjusting attack density and insect density under the bark. Non-host volatiles are repellent to *I. typographus*, so that beetles do not waste energy boring into non-host trees. The relationship between host resistance, pheromone compounds and behavior, non-host volatiles, bioassays and mass trapping are reviewed. Results of field bioassays stressed that traps baited with specific pheromones could be used as a reasonable protection measure.

Keywords: *Ips typographus*; Pheromone; Aggregation pheromone; Parasitoids; Predator; Non-host volatiles; Control and management

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Introduction

Ips typographus (L.), distributed throughout the Palearctic region (Weslien 1992), is one of the most damaging bark beetles native to Europe, and is intercepted frequently in wood packing material moved internationally from Europe. Outbreaks of *I. typographus* have caused great damage to Norway spruce (*Picea abies* (L.) Karst.) forest in Europe (Ravn 1985). Among the European *Ips* species attacking *Picea* spp., *I. typographus* is probably the most aggressive. Either physiological weakening of forest or an extreme increase in beetle populations may cause mass attack.

The process of host colonization can be divided into four phases: dispersal, selection, concentration, and establishment (Wood 1982). Males initiate host colonization and produce a mixture of semio-chemicals which attract males and females. During epidemics, they mass attack living tree, and overcome host resistance. An individual male will accept up to five females (Hednen and Schroeder 2004) after he has excavated a nuptial chamber in the phloem under the bark.

Chemical ecology

Ips typographus and its host

Several studies have been done on the relationship between

monoterpene hydrocarbons presented in host trees and oxygenated monoterpenes found in the hindgut of *I. typographus* (Birgersson 1989; Leufvén and Bergström 1987; Baier 1996). Mass attack of *I. typographus* is caused by one or two factors (Bakke 1983): (1) an abundance of mature, susceptible host trees, physiological weakened by storm-felling or drought; and (2) extremely high population level of *I. typographus*. When pioneer *I. typographus* bore into a host tree, they first meet primary resin stored in the inner bark and phloem of the tree as a preformed defense system; this resin is rich in monoterpenes and acts as a first line of defense (Shrimpton 1973). If smaller bark beetle populations infested healthy trees, mass attack would be prevented by resistance of the host trees. The resin exuded by host trees in response to a bark beetle attack contains monoterpene hydrocarbons that are somewhat toxic to both the bark beetles (Trapp and Croteau 2001) and their associated microorganisms. Volatile monoterpenes in the resin serve as species-specific chemical cues in host location (Wood 1982).

Considerable amounts of yeast (*Ceratocystis* type fungi) associated with *I. typographus* were found in beetle galleries (Christiansen and Horntvedt 1983) one week after attack, and blue stain developed after several weeks (Whitney 1982). The blue stain fungus vectored by the beetle initiates secondary defenses of the host, producing more resin (Christiansen and Horntvedt 1983). The host produces more resin to defend the attack, and the amount of monoterpenes surrounding the galleries increases about ten-fold in the phloem compared with unattacked areas (Leufvén and Birgström 1987). Commonly, a resistant tree produces more resin and last a longer time than a susceptible tree (Birgersson 1989). Francke & Vite (1983) hypothesized that the ultimate exploitation of these detoxification products as pheromone cues probably represents a complex evolutionary adaptation between *I. typographus* (L.) and its host. Trapp & Croteau (2001) assumed that the benefits of utilizing specific semio-

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Biography: SUN Xiao-ling (1974-), female, Ph. Doctor Candidate in School of Forestry, Northeast Forestry University, Harbin, 150040, P.R. China.

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chemical signals to locate a suitable host must outweigh the disadvantages.

Baier (1996) studied correlations of the defense reactions of Norway spruce of different vigour levels in response to controlled attacks of *I. typographus*. Some data showed that higher proportions of spruce trees older than 80 years enhanced bark beetle for the attack of stands, with trees over 100 years being most susceptible. Brignolas *et al.* (1998) suggested that phenolic composition in phloem could be used to predict Norway spruce resistance to *I. typographus* and their associated fungi. Wound response of host tree, triggered by bark beetles and associated pathogenic fungi, is characterized by accumulation of antifungal compounds, increased terpene concentrations, and morphological changes (Viiri *et al.* 2001), which are toxic to bark beetles and assist in wound healing.

Pheromones and behavior (Table 1)

The use of male produced attractants by *I. typographus* for

synchronization of mass attack was first shown by Bakke (1970). Vité *et al.* (1972) also reported the monoterpene alcohols: *cis*-verbenol (cV), *trans*-verbenol (tV), Ipsdienol (Id), and Ipsenol (Ie) in the hindguts of males. Bakke (1976) reported that male hind-guts contained equal amounts of tV and cV when initiating attack; Id was also present in males when boring the nuptial chamber, and Ie appeared in the hind-gut of males after females started oviposition; verbenol isomers were produced when males were exposed to oleoresin or α -pinene. However Birgersson *et al.* (1984) detected Ie and Id in males only after females were accepted, and the amounts increased after oviposition. Verbenone (Vn), MB, cV and tV, myrtenol (Mt), *trans*-myrtenol (tM), Id, Ie and 2-phenylethanol (PE) were identified in the hindguts of *I. typographus* from eight different attack phases on *P. abies*. Neither Id nor Ie was detected in offspring of either sex of *I. typographus* (Anderbrant *et al.* 1985). Subsequent studies confirmed that Id and Ie were found only in mated males (Birgersson *et al.* 1988).

Table 1. Pheromone candidates of *Ips typographus*

| Abbreviation | Compounds (MW) | Precursor | Origin | Behavior role | References |
|--------------|---------------------------|--|---|---|--|
| cV | <i>cis</i> -verbenol | (-)- α -pinene | Males hindguts from natural attacks on <i>Picea abies</i> ; trace amounts found in female hind-guts | Primary aggregation pheromone / Kairomone | Vité <i>et al.</i> 1972; Bakke <i>et al.</i> 1977; Birgersson <i>et al.</i> 1988; Klimetzek and Francke 1980; Bakke and Kvamme 1981 |
| tV | <i>trans</i> -verbenol | (+)- α -pinene | Males hindguts from natural attacks on <i>Picea abies</i> ; trace amounts found in female hind-guts | Play a part in regulating the density of attack/Kairomone | Vité <i>et al.</i> 1972; Bakke <i>et al.</i> 1977; Birgersson <i>et al.</i> 1988; Klimetzek and Francke 1980. |
| Id | Ipsdienol [(R)-Ipsdienol] | myrcene | Males hindguts from natural attacks on <i>Picea abies</i> | Aggregation pheromone/Kairomone | Vité <i>et al.</i> 1972/ Bakke <i>et al.</i> 1977; Birgersson <i>et al.</i> 1984; Bakke and Kvamme 1981; Schlyter <i>et al.</i> 1992 |
| Ie | Ipsenol | Id | Males hindguts from natural attacks on <i>Picea abies</i> | Play a part in regulating the density of attack/Kairomone | Vité <i>et al.</i> 1972; Bakke 1976; Birgersson <i>et al.</i> 1984; Birgersson <i>et al.</i> 1988; Bakke and Kvamme 1981 |
| MB | 2-ethyl-3-buten-2-ol | Under a stricter hormonal or nervous control (CNS) | Males hindguts from natural attacks on <i>Picea abies</i> (male specific) | Primary aggregation pheromone, promote landing | Bakke 1976; Bakke <i>et al.</i> 1977; Birgersson <i>et al.</i> 1984. |
| Vn | verbenone | cV and tV | Males hindguts from natural attacks on <i>Picea abies</i> | Anti-aggregation pheromone | Birgersson <i>et al.</i> 1984; Bakke 1981; Leufvén, A. <i>et al.</i> 1987 |
| Mt | myrtenol | α -pinene | Males hindguts from natural attacks on <i>Picea abies</i> ; trace amounts found in female hind-guts | A product of detoxication | Birgersson <i>et al.</i> 1984, 1988 |
| tM | <i>trans</i> -myrtenol | β -pinene | Males hindguts from natural attacks on <i>Picea abies</i> ; trace amounts found in female hind-guts | A product of detoxication | Birgersson <i>et al.</i> 1984 |
| PE | 2-phenylethanol | — | Males hindguts from natural attacks on <i>Picea abies</i> | Primary aggregation pheromone | Birgersson <i>et al.</i> 1984 |
| — | β -isophorone | — | Only found in females hindguts from natural attacks on <i>Picea abies</i> | — | Birgersson <i>et al.</i> 1984 |
| — | α -terpineol | — | Trace amounts found in females hind-guts | — | Birgersson <i>et al.</i> 1984 |

Note: “—” in the table means the literature reviewed didn't mention that.

Bakke *et al.* (1977) suggested that MB and cV were the primary aggregation pheromones of *I. typographus*. Methylbutenol has been shown to promote landing (Schlyter *et al.* 1987b). Dickens (1981) suggested that MB was probably a short-range orientation and/or arrestment cues for *I. typographus*. Leufvén and Bergström (1987) reported that MB, together with Ie and Id, which is present in the guts, could not be detected in phloem

from gallery walls.

Some studies focused on exploring the olfactory mechanisms for avoiding intra- and inter-specific competition. Byers (1983) found *Ips* species had sex-specific responses to aggregation pheromones. In a simulation study, Byers (1984) found that *I. typographus* males required minimum spacing of about 2.5 cm between attacks to avoid intra-specific competition, and hy-

pothesized that part of the mechanism was avoidance of higher concentrations of male pheromones, which could have important consequences for terminating aggregation and mass attack during colonization. Anderbrant *et al.* (1985) found there was a relationship between the amount of pheromones in the hind-gut of male offspring and attack densities. Schlyter *et al.* (1987) studied the behavior of *I. typographus* in different attack phases, and found that the presence of females decreased pheromone production in males, which decreased the attraction of females but not males, this supported the hypothesis of Birgersson *et al.* (1984). The decreased attraction of females could switch attraction to adjacent trees, and the production of *Ie* and *Vn* would probably inhibit male attraction to the first colonized tree with its lower pheromone release playing a role as density-regulating signal (Schlyter and Löfqvist 1986). Byers (1989) speculated on the theoretical mechanism of attack density regulation and termination of aggregation in *I. typographus* during colonization on a host tree. Schlyter *et al.* (1992) found that response of *I. typographus* and *I. duplicatus* to their respective pheromones showed a good separation during mass-attack with only a initial cross-attraction. Byers (1993) found that chalcogran and methyl (*E, Z*)-2,4-decadienoate inhibited the attraction of *I. typographus* to MB and *cV*, similarly *Vn* inhibited response of *P. chalcographus* to its pheromone.

Individual variation in pheromone production and response

After Alcock's (1982) seminal paper, the evolutionary background of aggregation pheromones of *I. typographus* was examined in a perspective of individual selection. In the very first study on individual variation in content of pheromone components in bark beetles, Birgersson *et al.* (1984) found that both MB and *cV* varied greatly in amounts and relative proportions among individual males. Female beetles had *tV* and traces of most other components found in males plus a female-specific compound, β -isophorone, when accepted by the male. Birgersson *et al.* (1988) reported that the relative amounts of *cV*, *tV*, *Mt*, and *tM* varied little among males attacking the same spruce tree but varied greatly among males from different trees. Anderbrant *et al.* (1985) found the amounts of MB, *cV* and 2-phenylethanol in male hind-guts were lower in offspring obtained from high densities than low densities.

Birgersson *et al.* (1988, 1989) concluded that quantities of pheromone components were influenced by several external and internal factors in individual bark beetles. External factors include: sampling regime, monoterpene composition in different host trees, within-tree resin flow, spatial or temporal differences in the enantiomeric composition of host tree resin, and variation in resin production of host trees (host tree resistance). Internal factors include: mating status, genetic variation, individual quality (determined by the attack density during their brood period), and history of the individual beetles.

Pheromone biosynthesis

Birgersson *et al.* (1984) classified hind-gut volatiles into 3 groups: MB; the pinene alcohols including *tV*, *cV*, *Mt*, *Vn*, *tM*, and 2-phenylethanol; and Ipsdienol-Ipsenol.

Methylbutenol

Methylbutenol is an essential compound in the attractive lure for *I. typographus* (Bakke *et al.* 1977). Beetles given fight exercise had larger amounts of MB present in their hindguts than cold-stored ones. The production of MB may be under stricter

hormonal or nervous (CNS) control, stimulated by the males excavating behavior (Birgersson *et al.* 1988), because appreciable amounts of MB were found in empty hindguts, and variation in MB could not be explained by variation in host monoterpenes (Birgersson *et al.* 1984). The quantitative difference between males in the early versus late attack phase is larger than between males from different host trees (Birgersson 1989), and the production of MB without feeding could be enhanced by the application of juvenile hormone (Hackstein and Vité, 1978). Although MB is not assumed to be a metabolite derived from host tree monoterpenes, the production of MB may be induced by the production of defensive compounds by the host (Birgersson 1989).

Pinene alcohol group

Compounds in the pinene alcohol group are present in the highest amounts after males have bored completely into the phloem, and all are derived from a pinane skeleton, except 2-phenylethanol (Birgersson *et al.* 1984). Vité *et al.* (1972) suggested that the biosynthesis of *cV* and *tV* was triggered by exposure to host tree oleoresin. The almost parallel increase and decrease in the amounts of *tV*, *cV*, *Mt*, and *tM* in the gut of male *I. typographus* in various phases suggest that they originate in the same biochemical pathway (White *et al.* 1980). However the studies of Birgersson *et al.* (1984) and Anderbrant *et al.* (1985) support the hypothesis that verbenols are produced by two separate biosynthetic pathways working in parallel (Birgersson *et al.* 1988). Leufvén *et al.* (1987) supposed that *cV* and *tV* were produced mainly by the bark beetles, and that *Vn* was probably produced mainly by yeast present in the galleries. The production of *cV* in attacking males continues until the production of the host defensive resin ceases. Birgersson *et al.* (1989) assumed that all the *cV* released from galleries was produced by the beetles.

Earlier studies by Renwick *et al.* (1976), and Byers (1981) showed that the production of *cV* and *tV* by *Ips* species depended on the amount and enantiomeric composition of the precursor (α -pinene), but *Mt* production was much less affected by the enantiomeric composition of the precursor. Birgersson *et al.* (1988) verified that production of *cV* was not correlated with flight exercise, but instead with the amount of (-)- α -pinene in the host. The relative amounts of *cV* and *tV* in male *I. typographus* hindguts corresponded very closely to the proportion of (-)-(2S, 5S)- and (+)-(2R, 5R)- α -pinenes in the phloem (Lindström *et al.* 1988). The verbenols can be further oxidized to (+)-verbenone and (-)-verbenone, which have been shown to act as anti-aggregation pheromones (Borden *et al.* 1984).

Ipsdienol and Ipsenol

Ipsdienol and *Ie* are characteristic of the *Ips* genus (Wood 1982), and are found only in mated males (Birgersson *et al.* 1988). *Ie* is not detected when *Id* is at a maximum (Birgersson *et al.* 1984), which supported the hypothesis by Hughes (1974) and Fish *et al.* (1979) that *Ie* is produced from *Id*. Variation in connections of *Ie* and *Id* were not significantly correlated with any host monoterpene (Birgersson *et al.* 1984), indicating that *Ips* bark beetles, probably synthesize pheromones de-novo.

Inhibition by nonhost volatiles

In recent years, studies have found that volatiles from nonhost bark and green leaves inhibit the response of *I. typographus* to their aggregation pheromones. Byers *et al.* (1998) found that

green-leaf volatiles (GLV) from birch, (Z)-3-hexen-1-ol and 1-hexanol reduced attraction of *I. typographus* and *P. chalcographus* to their aggregation pheromones, and suggested this behavior was adaptive because bark beetles avoided wasting time on nonhost trees. Zhang *et al.* (1999a) analyzed nonhost GLV from *Betula pendula*, *B. pubescens*, *Populus tremula*, and *Sambucus nigra*, found that *I. typographus* antennae responded strongly to (Z)-3-hexen-1-ol, 1-hexanol, and (E)-2-hexen-1-ol. A blend of these three GLV alcohols plus Vn reduced catch of *I. typographus* in pheromone-baited traps by 95%. Zhang *et al.* (2000, 1999b) found that nonhost bark volatiles as well as GLV could be used as long-range olfactory cues by *I. typographus*. Zhang (2003) found that binary, ternary or quaternary combinations of *trans*-conophthorin, 3-octanol, 1-octen-3-ol and Vn significantly reduced attraction to aggregation pheromones, trap catches could be reduced by 50%-70% by individual non-host volatiles (NHV).

Field trapping bioassay and application of pheromones for survey and control of *Ips typographus*

In field trapping experiments, Bakke *et al.* (1976) found that Id plus cV or tV and α -pinene was the most attractive lure blend, catching about five times as many beetles as other combinations. Bakke *et al.* (1977) subsequently reported that MB, combined with cV and Id produced the highest trap catches. Response was not enhanced by the addition of α -pinene, β -pinene and myrcene. High concentrations of aggregation pheromones, especially cV, were found to reduce the aggregation on the bole of host trees (Schlyter *et al.* 1987). Krawielitzki *et al.* (1977) first verified that optical pure (S)-cV was responsible for aggregation. Bakke (1981) hypothesized that Vn (both enantiomers) counteracted the effect of the aggregation pheromone and shifted the attack to un-infested bark areas on the tree under attack or to neighboring trees. Bakke *et al.* (1983) compared catching effect of a number of trap designs. Schlyter *et al.* (1992) tested the response of *I. typographus* to various combinations and release rates of aggregation pheromone candidates in field trapping bioassay. The results supported the hypothesis that MB and cV were the primary aggregation pheromones of *I. typographus* (Bakke *et al.* 1977). That catch of *I. typographus* was increased by the addition of primary host attractants to traps baited with aggregation pheromones was found by some experiments. Schlyter *et al.* (1987) studied the different roles of cV, MB and Id, provided support for the idea that each pheromone component has a different role in eliciting steps in a behavioral subsequence. Application of Vn and Id significantly reduced attack density of *I. typographus* on trapping logs, regardless of reduction rates but turpentine had no inhibitory effect (Bakke 1987).

Lots of studies have focused on the influence of host volatiles on attraction of *I. typographus*. Tomescu *et al.* (1979) showed that α -pinene synergized attraction to the blend of MB, cV and Id in laboratory bioassays. Jakuš and Blaženec (2003) found that attraction could be increased by having a lower relative percentage of cV and by supplementing a certain percentage of MB with (-)- α -pinene.

Actually, the catch of different sexes of *I. typographus* is influenced by numerous factors. Bakke (1983) suggested that Id not only increased catch in traps baited with cV and MB, but also increased the relative proportion of females. Schlyter *et al.* (1987) reported that the proportion of males in pipe traps was reduced

when high dose of cV were introduced to pheromone mixtures. Jakuš and Blaženec (2002) found that the proportion of males was higher in pheromone trap barriers than in single traps, and suggested that the difference was related to different percentages of cV in the pheromone baits. Jakuš and Blaženec (2003) also found that an increased in the percentage of (-)- α -pinene increased the percentage of males caught in single traps.

Use of pheromones in detection, control and management of *Ips typographus*

Pheromones were introduced into the control program of *I. typographus* in Europe in 1978 (Weslien 1992) and an extensive mass-trapping control program was initiated in 1979. Bakke (1982) used mass trapping as part of an integrated control program to suppress population of *I. typographus* in Norway. Since 1983, the use of traps against *I. typographus* was broadly practiced in the integrated control system. Eidmann (1983) discussed the methods of using pheromones to manage *I. typographus* in Scandinavia. Austarå *et al.* (1986) reported that addition of some host volatiles in the pheromone trap system might improve their effectiveness in beetle management programs. Babuder *et al.* (1996) compared the selectivity of synthetic aggregation pheromones Linoprax® and Pheroprax® in black flight barrier traps and suggested the establishment of a pheromone-based mass-trapping program for bark beetles in timber storage yards. Dimitri *et al.* (1992) evaluated the influence of mass trapping on the population dynamics and damage of bark beetles. Byers (1993) suggested that the effective attraction radius was about 2 m for a specific release rate of synthetic pheromones.

Subsequently, Weslien (1992) investigated the effects of mass trapping on *I. typographus* (L.) populations and showed that capture rate was about 30% while tree mortality rate declined about 80%. Niemeyer (1997) examined the experiences and problems of integrated control of *I. typographus* in Northern Germany, and declared that the complete control system with well applied traps reduced the successful infestation of living spruce by 70%-100% compared with systems without traps. So, traps baited with specific pheromones could be used as a reasonable protection measure.

Response of natural enemies to *I. typographus* pheromones

Natural enemies play an important role in suppressing populations of *I. typographus* (Wermelinger 2002). Weslien (1992) estimated that natural enemies could reduce reproduction of *I. typographus* by 83%. Raffa and Dahlsten (1995) suggested that predators and parasites strongly influence the population and behavioral ecology of bark beetles, and natural enemies can rapidly orient to suitable habitats and hosts by the cues associated with herbivore metabolism, communication, and feeding.

Natural enemies of *I. typographus* are attracted to its pheromones. Bakke and Kvamme (1978, 1981) revealed that synthetic Id, Id and (s)-cis-verbenol, either individually or in combinations functioned as kairomones for the *I. typographus* predators, *Thanasimus formicarius* (L.) and *T. femoralis* (Zett.); MB elicited no response. Zurr (1985) supported this conclusion. *Thanasimus formicarius* larvae are thought to cause high levels of brood mortality in *I. typographus* (Mills 1985; Weslien and Regnander 1992; Weslien 1994). Mills and Schlup (1991) investigated the

short range host location mechanisms of *Coeloides bostrychorum* Gir., *Dendrosoter middendorffii* (Ratz.) and *Rhopalicus tutela* Walk, three parasitoids of *I. typographus*, and suggested that volatiles are probably proximal cues used for host location. Subsequently, Babuder *et al.* (1996) confirmed that some predators of *I. typographus* were attracted to pheromone traps, and he concluded that the present synthetic pheromones can not completely prevent catches of predators and other useful insects.

Aspects of *Ips typographus* semiochemistry and behavior that require further research

Based on the review, these 5 projects will be high-lighted in the near future in China:

(1) Because the same species in different geological habitats maybe have different pheromone system, so more detailed chemical analysis of *I. typographus* pheromones in different habitat should be carried out.

(2) Role of *I. typographus* pheromones, to target beetles and especially to other insects, which live in the same ecological inch, should be studied.

(3) Extensive investigation on the species of predators and parasitoids in different stands should be carried out, in order to better apply biological control management.

(4) Chemical analysis of host volatiles from Chinese *Picea spp.* and bioassays (both in lab and field) should be performed to find the role of chemical cues in host location of predator and parasitoids.

(5) The chemical mechanism of host location should be studied further.

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